Mastozoología Neotropical, 20(2):367-372, Mendoza, 2013
Versión impresa ISSN 0327-9383
Versión on-line ISSN 1666-0536

http://www.sarem.org.ar

Nota

INTER-FEMALE TERRITORIAL BEHAVIOR IN PAMPEAN GRASSLAND MOUSE, *Akodon azarae* (CRICETIDAE: SIGMODONTINAE)

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ABSTRACT. In order to study territorial behavior in *Akodon azarae* females we performed 15 resident-intruder tests between breeding females in 30 individual enclosures. Each enclosure was provided with water and food ad libitum, and shelter. Aggressive behavior infrequent and did not vary between residents and intruders. Resident and intruder spent most of the time exploring the environment, suggesting tolerant coexistence. Our results did not provide evidence of territorial behavior in females, and contradict inter-female spatial avoidance registered in previous studies. We propose future resident-intruder tests including the nest site as defendable resource and a longer previous permanence period in individual enclosures.

RESUMEN. Comportamiento territorial entre hembras del ratón del pastizal pampeano, *Akodon azarae* (Cricetidae: Sigmodontinae). Para estudiar territorialidad en hembras de *Akodon azarae* realizamos 15 enfrentamientos entre residentes e intrusas dentro de 30 clausuras individuales. Cada clausura contó con agua, alimento y refugio. El comportamiento agresivo fue muy poco observado y no varió entre residentes e intrusas. La mayor parte del tiempo las hembras exploraron el entorno, sugiriendo una convivencia tolerante entre ellas. Nuestros resultados no provén evidencias de territorialidad en hembras, contradiciendo la evitación espacial entre hembras registrada en estudios previos. Proponemos realizar pruebas entre hembras residentes-intrusas que incluyen al sitio de nidificación como recurso defendible, aumentando además el tiempo de residencia de las contrincantes.

Key words: Aggressiveness. Resident-intruder test. Resources. Territory.

Palabras claves: Agresividad. Prueba de residente-intruso. Recursos. Territorio.

Mating systems of species should represent the outcome of reproductive strategies of individuals (Trivers, 1972; Clutton-Brock, 1989). Since each sex has different constraints on reproduction, males and females generally have evolved different strategies for mating to maximize reproductive success (Kokko and Jennions, 2008; Aloise King, 2013). Because gestation and lactation basically emancipate males from having to provide parental care (Emlen and Oring, 1977), polygyny and promiscuity have been considered the predominating mating systems in voles and mice (Wolff and Macdonald, 2004; Waterman, 2007). In polygynous mating systems, males and females use space differently: males have larger home ranges than females and mutually exclusive home ranges that extensively overlap with more than

Recibido 27 marzo 2013. Aceptado 4 julio 2013. Editor asociado: M Busch

one female's home range, and females may be territorial or not (Wolff et al., 1994). Females invest more in their offspring undertaking high costs associated with pregnancy, lactation and young guarding, and typically compete with each other for food and space to rear offspring (Emlen and Oring, 1977). Thus, territoriality of females has been proposed as an adaptation for defense of food resource (Ostfeld, 1985, 1986, 1990; Tamarin et al., 1990). However, Wolff and Cicirello (1991) and Ylönen et al. (2004) suggest that territoriality of female mice and voles is mainly directed towards other adult females which are more likely to commit infanticide than adult males.

Akodon azarae (Cricetidae: Sigmodontinae) has a polygynous mating system, with offspring cared exclusively by females (Suárez, 1996; Suárez and Kravetz, 1998; Bonatto et al., 2012). Reproductive success of *A. azarae* females is determined by its ability to get green cover and food, whereas success of a male depends upon its ability to copulate with females (Bonaventura et al., 1992). During the breeding season *A. azarae* females have lower home ranges than males (Priotto and Steinmann, 1999; Bonatto et al., 2012) and show smaller movement distances than males (Gomez et al., 2011). In previous studies, Priotto and Steinmann (1999) and Bonatto et al. (2012) found that during the breeding period, breeding females of *A. azarae* keep exclusive home ranges. In these studies female territoriality was presumed from the exclusive use of space. This means, as suggested by Batzli and Henttonen (1993), that when home range overlap is significantly lower than it would be expected by random placement, individuals are avoiding one another. Taking into account that *A. azarae* females are more sensitive than males to food and cover their territorial behavior would lead them to maintain exclusive reproductive spaces to guarantee these resources. Considering that territoriality includes aggressive behaviors by territory owners against intruders (Barnett, 1975), the aim of this study was to test the prediction that during the breeding period resident females are more aggressive than intruder females.

This study was carried out on the Reserva El Espinal in the Universidad Nacional de Río Cuarto Campus (33º 07' S; 64º 14' W), Córdoba, Argentina, located in a natural pasture comprising herbaceous weedy species interspersed with woody shrubs, with high percentage of gramineous cover uniformly distributed. All these characteristics are typical of natural habitats of *A. azarae*. From December 2010 to February 2011 we collected females of *A. azarae* from an area located 30 km away from the study location, along road borders and borders between cultivated fields and pastures. We studied inter-female aggression in thirty 0.79 m^2 round individual enclosures (called territories) placed in the Reserva El Espinal. Each enclosure was limited by a concrete circle of 1 m diameter and 0.5 m high, covered with an iron mesh. Each territory was provided with water, rodent laboratory chow, and sunflower and maize seeds ad libitum. Besides, we provided oakum as nesting material, and one open and locked live trap covered with leaf litter as refuge.

We performed 15 encounters between 30 different breeding females (females with perforated vagina, and females simultaneously pregnant and suckling) of similar weight (25 g ± 2 g). To test our prediction we used the resident female behavioral response towards an intruder female. To comply with the resident-intruder paradigm (Barnett, 1975), and according with Bester-Meredith and Marler (2001, 2003, 2007) and Bonatto et al. (2013), 48 hrs prior to the behavioral tests females were placed individually into enclosures. For each inter-female trial we distinguished two female conditions: territory resident (female housed in the enclosure where the encounter was performed) and territory intruder (intruder in the enclosure in which the encounter was made). Animal condition (resident/intruder) was randomly assigned before each trial. To perform encounters we placed into an enclosure a movable polycarbonate Circular Opaque Arena (COA), of 70 cm high (20 cm higher than enclosure border), 219.8 cm perimeter and 70 cm diameter, with an open ground area (Bonatto et al., 2013). A removable opaque partition was placed across the centre of the COA at the beginning of each trial, and females (resident and intruder) were placed simultaneously on either side of the partition for a 1-min acclimation period. After this

period the separator was carefully removed so that interactions between contestants could occur, and then the resident-intruder test started. Before the encounter, to identify the opponents, one of them was marked on its forehead with an odorless yellow watercolor highlighter that did not affect individual behavior in small rodent species (Korpela et al., 2011). Trials were performed during one of the activity peaks of the Pampean grassland mouse, between 09:00 and 11:00 am (Priotto and Polop, 1997). In this study animals were used only once.

Each encounter lasted five minutes and was recorded using a video camera. Behaviors observed during encounters are described in **Table 1**. The different types of behavior were classified as interactive and non-interactive. We measured each behavior per encounter and for each opponent as duration (in seconds) of a determined behavior along the five minutes (maximum duration value for a given behavior = 300s). For statistical analyses we grouped the different behavior types in four categories (**Table 1**): aggressive behavior (AA, At, AP, P), submissive behavior (Sb, A, Es), amicable behavior (Sp, Ss), and non-interactive behavior (Ex, Q, G). In order to pool all females for the statistical analyses we first analyzed reproductive condition (open vagina, pregnant, and sucking) using a Mann-Whitney *U*-tests (One-tailed test, a = 0.05) for each behavioral category. Due to the fact that the duration of aggressive, submissive, amicable and non-interactive behaviors did not vary in relation to female reproductive condition (One-tailed test, a = 0.05; aggressive: $U = 105.5$, N = 30, $P = 0.41$;

Table 1

Behaviors observed between resident and intruder *Akodon azarae* females during paired encounters in enclosure conditions.

Interactive behaviors
Aggressive approach (AA): Directional and fast locomotion towards the opponent, often combined with pilo-erection. This behavior may end with intentional movements of boxing and biting.
Attack (At): Rushing and leaping at the opponent with kicks and bites.
Aggressive posture (AP): The animal stands on four feet and tenses its body towards the opponent, pointing the nose at it. Generally this posture ends in attack.
Pursuit (P): Running after the opponent attempting to bite and chase it.
Submissive posture (Sb): This behavior is assumed in response to an attack or an aggressive posture of the opponent. The animal bends its neck laterally, offering the concave side to the opponent, generally with flexion of the contralateral forelimbs, ears down, eyes closed or nearly closed.
Alert (A): Individual remains quiet in one place in attitude of alertness, ears down, maintaining permanent visual contact with its opponent. Generally accompanied by body shakings and sniffing.
Escape (Es): This behavior is exhibited in response to a pursuit. Rapid locomotion directed away from the opponent, generally accompanied by squeaks.
Sniffing partner (Sp): Individual either stands close to or follows the partner, while sniffing the oral or genital region of the opponent.
Sharing space (Ss): Opponents stay close by and share a common space within the COA. This behavior may include grooming of the opponent.
Non interactive behaviors
Exploratory behavior (Ex): Vertical and horizontal environment exploration, individual exploratory movements in all directions along the ground or climbing the lateral fence of the COA. This includes any behavior in which the animal explores anything of the environment ignoring the other animal.
Quiet (Q): The animal lies down or stands motionless except for occasional chewing movements, ignoring the other animal.
Self grooming (G): Grooming or manipulation of any part of the own body with mouth or forelimbs.

submissive: $U = 105.5$, N = 30, $P = 0.41$; amicable: $U = 28$, N = 30, $P = 0.27$; non-interactive: $U = 28$, N = 30, $P = 0.27$), we were able to pool all the females. Thus, we analyzed each behavioral category in relation to resident or intruder condition using one-tailed Mann-Whitney *U*-tests. Statistical analyses were carried out using R version 2.12.2 (R Development Core Team).

In female-female encounters the aggressive behavior was infrequent and did not vary between resident and intruders ($U = 96$, N = 30, $P = 0.49$; **Fig. 1**). Although the average time invested in submissive exhibitions by intruder females was fourfold greater than by resident females we did not find significant differences in the duration of this behavior between territory owners or intruders ($U = 143$, N = 30, $P = 0.20$; **Fig. 1**). During the encounters both resident and intruder females were equally amicable ($U = 116.5$, N = 30, $P = 0.88$; **Fig. 1**). Sniffing partner was the most common amicable behavior exhibited by both resident and intruder females. The non interactive category was the most common behavioral category observed in inter-female encounters. Even though resident females exhibited this behavior for longer than intruder females, the difference between female conditions was not statistically significant ($U = 91.5$, N = 30, $P = 0.40$; **Fig. 1**). In this category, exploratory behavior was the most common behavior exhibited by resident and intruder females; in all the encounters both residents and intruders spent most of the time performing vertical and horizontal environmental explorations. Self-grooming was another non interactive behavior commonly exhibited by both opponents.

In previous space use studies we proposed that *A. azarae* females were territorial based on the absence of home range overlap between females (Bonatto et al., 2012). In this study we assumed that females would perform aggressive behaviors associated with food and refuge defense. However, our results did not provide evidence of territorial behavior of females in association with the defense of their territories towards other females. Moreover, during the trials, both resident and intruder females spent most of the time exploring the environment, suggesting tolerant coexistence. Thus, our results contradict inter-female spatial avoidance registered both in natural and semi-natural conditions, as well as at low and high population densities (Priotto and Steinmann, 1999; Bonatto et al. 2012; Bonatto et al., personal obs.; Avila et al., personal obs). In natural conditions the aggressiveness of a territory owner could lead to the exclusion of potential rivals. Besides, if food and refuge defense are directly related with residence duration (John-

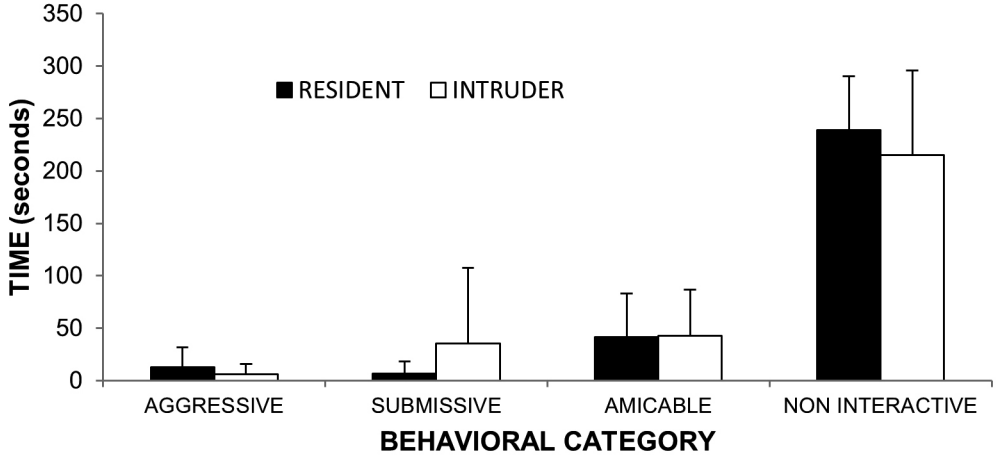

Fig. 1. Mean (+ SD) duration (in seconds) of each behavioral category in relation to condition of female (resident or intruder) in inter-female encounters of *Akodon azarae*.

sson and Forser, 2002), the permanence of a female in its territory longer than the 48-hour period used in this study would increase its perception of territory value. Therefore, in wild populations the increased residence time of *A. azarae* females in their territories could lead to aggressive responses against other females that attempt to trespass their breeding territory boundaries. Future resident-intruder tests with a longer previous permanence period of the individuals in the enclosures could elucidate if *A. azarae* resident females are more likely to win encounters as a result of their greater investment and local experience in comparisons with the challengers.

Territoriality of *A. azarae* females as an adaptation for defense of nest site rather than for defense of food and shelter could be an alternative explanation for the absence of overlapping between females' home ranges. However, the low rates of postpartum estrous (13.4%) registered in previous studies (Bonatto et al., 2012, 2013) would not support this explanation, and future resident-intruder tests should be developed in individual enclosures between *A. azarae* females with their pups as a defensible resource.

Acknowledgements. This research was possible through the support of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and Secretaría de Ciencia y Técnica, Universidad Nacional de Río Cuarto (SECyT-UNRC).

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